Food Habits of Piranhas in the Low Llanos of Venezuela

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Biotropica is currently published by The Association for Tropical Biology and Conservation.

Food Habits of Piranhas in the Low Llanos of Venezuela[1]

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ABSTRACT

Eight piranha species (Characidae: Serrasalminae) coexist in streams and pools of the western Orinoco River Basin llanos. The species differ in adult size, body form, and relative abundance. Examination of some 1300 specimens collected over a seven-year period (1979–1985) showed that food habits and diet diversity usually change with age. Small juveniles of the abundant and widespread *Pygocentrus notatus* eat microcrustaceans and aquatic insects. Above 40 mm standard length (SL), they take small fish and chunks of fish flesh. Small juveniles (20–80 mm SL) of six species (*Serrasalmus altuvei, S. irritans, S. cf. elongatus, S. rhombeus, S. caribe,* and *Pristobrycon cf. striolatus*) specialize in fins of other small fishes, but by 80 mm SL their diets shift to small fish, pieces of fish flesh, and fins. However, all sizes of *Catoprion mento* eat scales. Considerable diet overlap among different piranha species in the same size classes suggests that plentiful food resources are not limiting. These savanna piranhas do not depend on fruits and seeds as has been reported for piranhas in flooded tropical rain forests.

RESUMEN

Ocho especies de caribes o pirañas (Characidae: Serrasalminae) coexisten en los caños y pozos de los llanos occidentales de la cuenca del Río Orinoco en Venezuela. Las especies difieren en el tamaño del adulto, morfología del cuerpo y abundáncia relativa. El análisis de unos 1.300 especímenes, colectados durante siete años (1979–1985) muestra que los hábitos alimentícios y la diversidad en la dieta normalmente varían con la edad. Juveniles pequeños de la especie mas diseminada y abundante, *Pygocentrus notatus,* consumen microcrustáceos e insectos acuáticos. Al superar los 40 mm de largo estandar (LE), comen pequeños peces enteros y pedazos de peces. Los juveniles pequeños (20–80 mm LE) de seis especies (*Serrasalmus altuvei, S. cf. elongatus, S. irritans, S. rhombeus, S. caribe,* y *Pristobrycon cf. striolatus*) se especializan en el consumo de aletas de peces pequeños. Pero al llegar a los 80 mm LE su dieta cambia a peces pequeños enteros, pedazos de peces grandes, y aletas. Individuos de todas las edades de *Catoprion mento* consumen escamas. El considerable traslape entre las dietas de individuos de diferentes especies de caribes correspondientes a un mismo grupo de tamaño, sugiere que el alimento es abundante y no limita las poblaciones. Estos caribes de sabana, no dependen tanto de semillas y frutos, como ha sido reportado para los caribes de la selva pluvial del Amazonas brasilero.

As many as eight species of piranhas (Characidae: Serrasalminae) coexist in open savanna or low llanos of Apure State, Venezuela. Piranhas often comprise a high percentage of both total fish biomass and numbers (Mago-Leccia 1970, Taphorn & Lilyestrom 1984), but little is known of their natural history. Their body form ranges from sharp snouted and long bodied to blunt headed and robust (Fig. 1).

Piranhas are said to be highly carnivorous, using their powerful jaws and sharp teeth to clip out bites of flesh from fishes and other vertebrates (*e.g.,* Eigenmann 1915, Myers 1972). However, recent studies (Roberts 1970, Goulding 1980, Machado-Allison & Garcia 1986) reveal high diet diversity for piranhas and their close relatives. Goulding's (1980) stomach analyses of seven piranha species from in and around the Rio Machado in Amazonia Brazil indicated that *Serrasalmus rhombeus* was mainly a piscivore that usually bit chunks of flesh out of large fish. The few available specimens of the five uncommon or rare species had fed heavily on seeds. Amazonian *Serrasalmus*

elongatus feed primarily on fins and scales (Roberts 1970, Goulding 1980), and some species of *Serrasalmus* of the La Plata drainage are also fin eaters (Sazima & Zamprogno 1985; Northcote *et al.* 1986a, b). Machado-Allison and Garcia (1986) examined 134 specimens and described ontogenetic morphological changes and diets of three piranhas from the llanos of Guárico State, Venezuela. They reported similar diets for 10–70 mm standard length (SL) juveniles of *Pygocentrus notatus, Pristobrycon cf. striolatus,* and *S. rhombeus*—primarily invertebrates, fish fins, and small seeds. However, juveniles longer than 70 mm SL showed interspecific differences. *Catoprion mento* is a specialized scale eater (Roberts 1970, Vieira & Géry 1979, Sazima 1984).

This study describes ontogenetic and interspecific differences in diets of eight sympatric piranhas taken from flooded savanna and associated streams in the western llanos of the Venezuelan Orinoco River Basin (Fig. 2). Species examined were *P. notatus, Serrasalmus altuvei, S. caribe, S. cf. elongatus, S. irritans, S. rhombeus, P. cf. striolatus,* and *C. mento.*

Piranha taxonomy is disordered; however, except for the smallest specimens, we believe we have successfully sorted out the different species present in the study area.
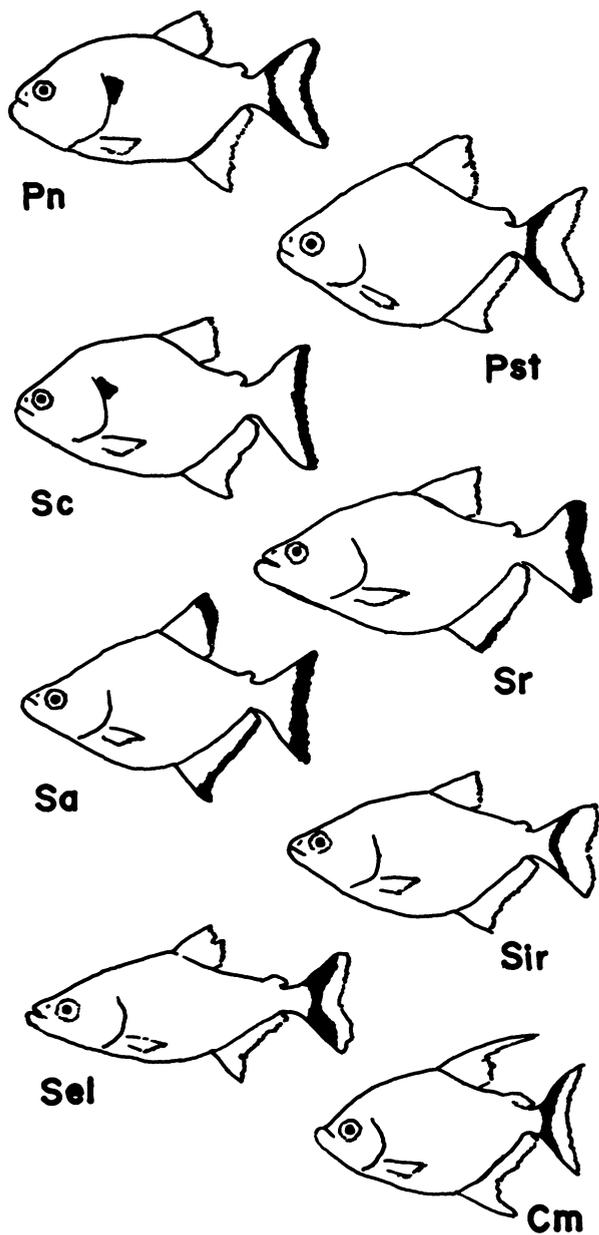
FIGURE 1. General body form and major fin patterns of eight species of piranhas, 55–70 mm SL, from study area in Apure, Venezuela: Pn = *Pygocentrus notatus,* Pst = *Pristobrycon cf. striolatus,* Sc = *Serrasalmus caribe,* Sr = *S. rhombeus,* Sa = *S. altuvei,* Sir = *S. irritans,* Sel = *S. cf. elongatus,* and Cm = *Catoprion mento.*

Some of the names used are provisional. A taxonomic review of the group is currently under way by Drs. William Fink and Antonio Machado. Recent helpful taxonomic studies of piranhas include Machado-Allison (1982; 1984a,

b) and Machado-Allison and Garcia (1986). Photographs of the species studied here are given in Nico and Taphorn (1986).

STUDY AREA

The Orinoco Llanos reach from the Orinoco River Delta in the east to the Andes Mountains. In Apure State, the low llanos are grassy floodplains subject to distinct wet and dry seasons resulting in pronounced seasonal changes in fish habitats. During high water (May–October) most of the area floods, but during the dry season standing water usually is limited to a few large permanent lagoons, large creeks, and rivers. Since the early 1970s, many earthen dikes have been constructed around vast areas of savanna. These dike systems or modules moderate the effects of seasonal water level changes within their boundaries and permit cattle ranching throughout the year. Dikes restrict local fish movements and have changed runoff patterns. Borrow pits are typically some 25 × 100 m and 1 to 2 m deep, but in many cases they stretch unbroken along entire dikes.

The UNELLEZ (Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora") Module (07°25'50"N, 69°35'30"W) is some 80 km west of Mantecal, Apure (Fig. 2). The 2.5-m-high dikes of the module surround a roughly rectangular area of 12,600 ha of open flat savanna whose terrain gradually slopes from west to east. Lower areas and deeper borrow pits contain water throughout the year, but usually are reduced to less than 0.5 m depth during the dry season. Their fish species composition resembles that of permanent lagoon habitats. During the rains most of the UNELLEZ module floods, with low areas covered by as much as 2 m of water.

Several large permanent creeks border the UNELLEZ module (Fig. 2). These low gradient streams have largely silt bottoms and are bordered by narrow gallery forests. Free-floating mats of vegetation, primarily *Eichhornia,* are common in stream and savanna pools. During high water, fishes can move between the streams and the module through culverts or breaks, but the interchange has been greatly reduced as dike stability has been achieved. During the late dry season (January to early April), Caño Maporal has little or no flow and is often reduced to isolated pools. Rainy season flow is continuous with depths to 5 m or more. Width ranges from 3 to 12 m during low water to over 20 m during peak flooding. Streams of the study area are essentially blackwater streams but with low transparency. During the first rains of the wet season they become very turbid, but clear as flow resumes. The flooded savanna pools are "whitewater," and usually very turbid, but in the late rainy season larger pools often become clearer.
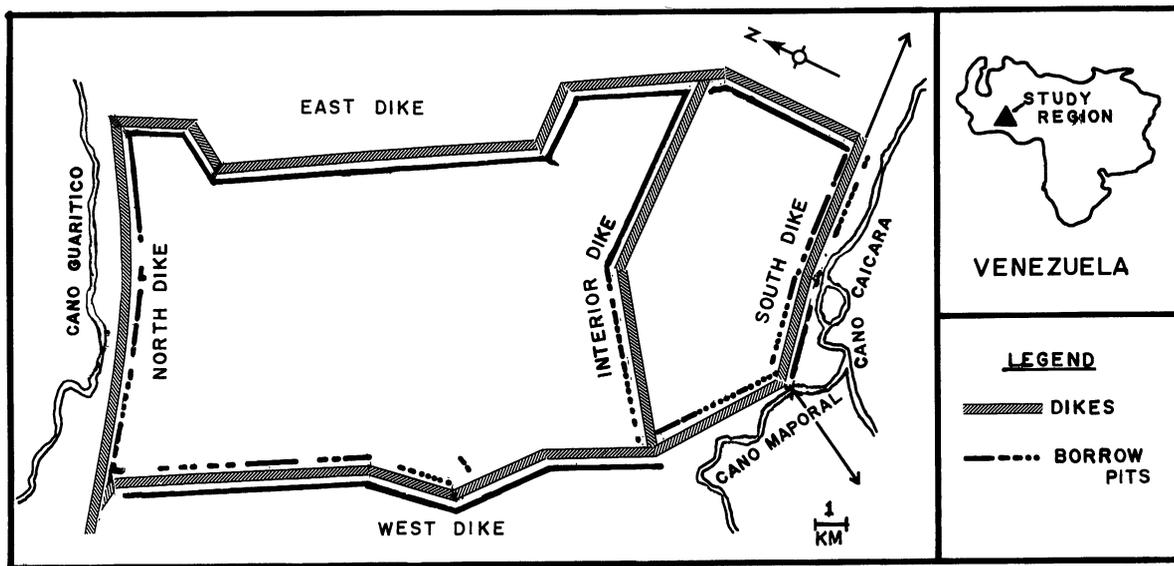
FIGURE 2. Map of study area in Apure, Venezuela, showing UNELLEZ module and major caños. Widths of dikes, borrow pits, and caños are exaggerated.

MATERIALS AND METHODS

About 200 fish collections were made in the UNELLEZ module and adjacent flooded areas and streams over a seven-year period (1979–1985). Collections were made during both low- and high-water periods and monthly in some years. Many specimens used were taken during a study of fish biomass (Taphorn & Lilyestrom 1984). Fishes were collected using cast nets, seines (10 × 2 and 5 × 2 m, mesh sizes 6 to >25 mm), hand nets, and hook and line. Most fishes were taken during daylight hours. A few of the largest fish were examined in the field, but most were preserved in formalin for later dissection.

Approximately 2000 piranhas were captured. We examined the stomach contents of 1248 and recorded frequency of occurrence (O), number (N), and dominance by bulk (D) for each food item. A partially subjective estimate of stomach fullness was made using scores from 0 to 3 (Thomerson & Wooldridge 1970): 0 if empty, 1 if significantly less than half full, 2 if about half full, and 3 if full. Adjusted volume (V), was derived from D and stomach fullness. That is, the dominant food category in a given stomach was assigned the fullness points (1–3) for that stomach. If two food items in a single stomach were of about equal volume, each received half the fullness value. Thus, %V = total fullness points for each food category as a percentage of all fullness points, and can be shown as

$$\%V = \left(\sum_{i=1}^{n} F_i \middle/ \sum_{i=1}^{n} T_i \right) \times 100$$

where F_i is the fullness points for stomachs whose dominant food item is F; T_i is total fullness points for all stomachs; and n is the number of stomachs examined of a species or size class.

Diet overlap values and dietary breadths were calculated (from V values) following Schoener (1970) and Levins (1968), respectively.

We used ten general food categories: (1) plant material—leaves, roots, small seeds, and filamentous algae; (2) decapods—crabs (*Dilocarcinus* sp.) and shrimp (*Macrobrachium* sp.); (3) microcrustaceans—copepods, cladocerans, ostracods and conchostracans; (4) aquatic insects—various families, including larvae and adults; (5) other invertebrates—mostly arthropods including terrestrial forms, but also aquatic nematodes and snails; (6) small whole fish—at least two-thirds of total body; (7) fish flesh—pieces of flesh bitten from fish; (8) fish fins—fins not taken with or attached to pieces of flesh; (9) fish scales—scales not taken with or attached to flesh; and (10) other—detritus, sand, nonfish vertebrates, and unidentifiable items.

Piranhas were divided into five size classes: Group I, 10–19 mm SL—small juveniles (probably all or mostly *P. notatus*); Group II, 20–39 mm SL; Group III, 40–79 mm SL; Group IV, 80–159 mm SL; and Group V, ≥160 mm SL. Several species were not represented in all size classes.

Almost all specimens examined are deposited in the Museo de Ciencias Naturales, UNELLEZ, Guanare, Venezuela, and in the Florida State Museum, Gainesville, Florida. Catalogue numbers are available from the authors

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TABLE 1. *Food items of Group I (10–19 mm SL) juvenile piranhas (most tentatively identified as* Pygocentrus notatus). *%O = percent frequency of occurrence (nonempty stomachs),* N = *mean number per nonempty gut, %D = percent dominance, %V = percent adjusted volume. 114 examined; 3 empty.*

Food items	%O	N	%D	%V
Plant material	5.4	nd[a]	—	—
Microcrustacea	91.0	27.5	54.8	58.1
Aquatic insects	73.0	3.4	37.9	36.9
Other inverts	12.6	0.2	4.0	2.3
Other	7.2	nd	3.2	2.7

[a] No data.

and from the two museums. Some names used by Nico and Taphorn (1986, *e.g.,* pp. 31 & 33) have been updated as follows: *Serrasalmus eigenmanni = S. irritans, Pristobrycon* sp. = *S. caribe,* and *Pristobrycon striatus = P. cf. striolatus* (W. Fink, pers. comm.).

In addition to stomach content analysis, we used mask and snorkel to observe piranhas in clearwater streams in the states of Bolivar, Guárico, and Monagas. Observations were also made of fish in aquaria.

RESULTS

The 114 stomachs of small juvenile piranhas (Group I) contained mostly microcrustaceans and aquatic insects (Table 1). Increased size within this group corresponded with a gradual switch from microcrustaceans to small aquatic insects. Primary food items, in order of importance (high %V and %D), were cladocerans, chironomid larvae, copepods, and ostracods.

Pygocentrus notatus (Lütken 1874).—*P. notatus* is the most abundant piranha in the llanos, occurring in both flooded savanna and flowing waters. This blunt-headed, heavy-bodied species (Fig. 1) reaches approximately 300

mm SL. Stomach contents of 516 *P. notatus* in the four larger size classes are given in Table 2 and Figure 3. Unlike most other piranha species, fish fins and scales were of minor importance in juvenile guts. Group II fish fed most heavily on aquatic insects, followed by microcrustaceans, but for Group III, fish flesh was the most important food item, followed by plant material (primarily vascular plant debris) and aquatic insects. Larger *P. notatus,* Groups IV and V, took mostly fish flesh and whole small fish.

Some 25 species of fishes (mostly characins) were identified from *P. notatus* Groups IV and V. Characins most frequently preyed upon were *Aphyocharax erythrurus, Ctenobrycon spilurus, Gymnocorymbus thayeri, Hemigrammus marginatus, Odontostilbe pulcher, Poptella orbicularis,* and *Roeboides dayi.* Others eaten included curimatids (*e.g., Curimata metae* and *Curimatella* sp.), lebiasinids (*Pyrrhulina cf. lugubris*), cichlids (*e.g., Microgeophagus ramirezi*), gymnotids (*e.g., Gymnotus carapo, Sternopygus macrurus,* and *Eigenmannia* sp.), auchenipterid catfishes (*Entomocorus gameroi* and *Parauchenipterus galeatus*), other catfishes (*e.g., Pimelodella* sp., *Hoplosternum littorale,* and *Hypophthalmus cf. edentatus*) and an unidentified annual cyprinodontid. Cannibalism by adults on small juveniles was also in evidence.

Larger juveniles and adults sometimes ate other vertebrates, perhaps as carrion. Different stomachs contained a chunk of flesh from a small caiman (*Caiman crocodilus*), skin of a mato lizard (probably *Ameiva*), and a small adult leptodactylid frog. Three individuals taken together had stomachs full of feathers, flesh, and bone fragments of a white-faced whistling duck (*Dendrocygna viduata*). Mammals were not found in *P. notatus* from the study area, but we have found flesh and fur of small rodents in specimens from nearby localities.

Serrasalmus irritans Peters 1877.—*S. irritans* is a very common piranha, usually second only to *P. notatus* in numbers of individuals. It has a moderately pointed snout

TABLE 2. *Food items of* Pygocentrus notatus *by size class. %O = percent frequency of occurrence (nonempty stomachs), %D = percent dominance, %V = percent adjusted volume.* N = *516.*

| Size class (mm SL)	II (20–39)			III (40–79)			IV (80–159)			V (≥160)		
No. examined	110			84			176			146		
No. empty	1			5			18			46		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	17.4	1.8	1.1	43.0	25.3	23.5	29.7	8.7	5.4	41.0	15.0	8.8
Decapoda	—	—	—	10.1	7.2	7.4	3.8	1.2	1.2	9.0	4.7	3.0
Microcrustacea	78.0	23.7	21.4	19.0	3.6	2.6	—	—	—	—	—	—
Aquatic insects	80.0	55.3	60.7	32.9	14.5	14.7	0.6	—	—	11.0	4.7	3.0
Other inverts	36.7	14.0	12.3	30.4	10.8	12.4	5.1	1.2	0.6	21.0	4.7	2.0
Sm whole fish	0.9	0.9	1.1	2.5	1.2	1.8	29.1	22.0	24.1	51.0	41.1	51.0
Fish flesh	0.9	0.9	1.1	29.1	19.3	25.3	81.6	59.0	63.7	38.0	17.8	20.5
Fish fins	—	—	—	36.7	8.4	4.1	12.0	0.6	0.3	7.0	2.8	1.8
Fish scales	—	—	—	17.7	2.4	1.8	12.0	4.6	2.8	12.0	3.7	2.0
Other	3.7	3.5	2.4	10.1	7.2	6.5	5.1	2.9	1.9	9.0	5.6	7.8
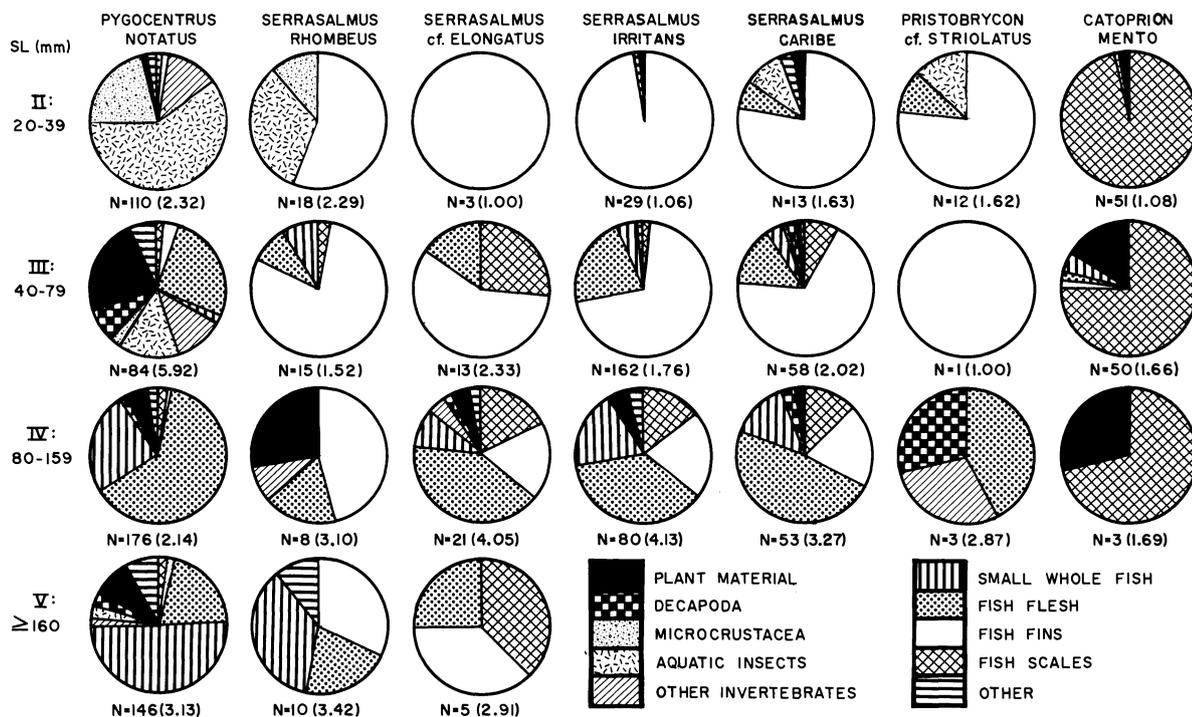
FIGURE 3. Diets by size class (II–V) of seven species of piranhas. Size of segments represents percentage of adjusted volume of each prey type. N = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).

(Fig. 1) and is seldom longer than 160 mm SL. A complex of two species may be involved (A. Machado-Allison, pers. comm.); however, we distinguished only one in the study area.

Our sample of 271 specimens (Table 3 and Fig. 3) shows that juvenile (Groups II and III) *S. irritans* specialized on fins of other fishes. Stomachs of the young of this piranha were typically packed with only fins, mostly of fishes smaller or similar in size to the predator. It was usually not possible to identify the fins eaten, but the thick red anal fins of *P. notatus* were found in two individuals. Large *S. irritans* preyed mostly on small whole fish, fish flesh, fins, and occasionally scales. Fishes eaten whole or in pieces by *S. irritans* included characids (*C. spilurus, O. pulcher* and *Hemigrammus* sp.), curimatids (*e.g., C. metae*), gymnotids, and cichlids (*e.g., M. ramirezi*). A small juvenile *P. notatus* was found in the stomach of one individual. No nonfish vertebrate remains were found.

TABLE 3. *Food items of* Serrasalmus irritans *by size class. %O = percent frequency of occurrence, %D = percent dominance, %V = percent adjusted volume.* N = 271.

Size class (mm SL) No. examined No. empty	II (20–39) 29 1			III (40–79) 162 7			IV (80–159) 80 10		
Food item	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	10.7	3.6	1.4	1.9	—	—	18.6	8.3	5.0
Decapoda	—	—	—	0.6	0.6	0.3	1.4	—	—
Aquatic insects	—	—	—	3.2	—	—	1.4	—	—
Other inverts	—	—	—	0.6	—	—	1.4	1.4	0.4
Sm whole fish	—	—	—	3.2	3.1	4.0	18.6	13.9	18.8
Fish flesh	—	—	—	21.9	17.5	21.0	28.6	25.0	37.1
Fish fins	92.9	92.6	97.3	81.9	73.8	72.3	37.1	22.2	21.3
Fish scales	10.7	—	—	23.2	3.1	1.3	37.1	23.6	14.2
Other	3.6	3.6	1.4	3.9	1.9	1.2	8.6	5.6	3.3

TABLE 4. *Food items of* Serrasalmus caribe *by size class. %O = percent frequency of occurrence (nonempty stomachs), %D = percent dominance, %V = percent adjusted volume. N = 124.*

Size class (mm SL)	II (20–39)			III (40–79)			IV (80–159)		
No. examined	13			58			53		
No. empty	0			2			3		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	7.7	7.1	3.2	16.1	1.7	1.6	26.0	5.8	2.9
Decapoda	—	—	—	1.8	1.7	2.4	8.0	1.9	2.9
Aquatic insects	7.7	7.1	9.7	—	—	—	—	—	—
Other inverts	—	—	—	5.4	1.7	0.8	4.0	—	—
Sm whole fish	—	—	—	5.4	3.4	4.0	14.0	9.6	13.7
Fish flesh	7.7	7.1	6.5	23.2	15.3	14.0	46.0	36.5	48.0
Fish fins	84.6	71.4	77.4	80.4	62.7	68.4	66.0	30.8	20.1
Fish scales	—	—	—	44.6	11.9	8.0	36.0	15.4	12.3
Other	7.7	7.1	3.2	1.8	1.7	0.8	—	—	—

Serrasalmus caribe Valenciennes 1849.—*S. caribe* is the third most common piranha in the study area. It is a medium-sized piranha, usually less than 160 mm SL. Its head shape is intermediate between the robust *P. notatus* and species with pointed snouts (Fig. 1). Unlike *Pygocentrus,* but similar to other *Serrasalmus,* it has a series of ectopterygoid teeth, easily seen even in small individuals (from about 25 mm SL). A total of 124 specimens were analyzed for diet (Table 4 and Fig. 3). It is primarily a fin eater when small (20–79 mm SL). The largest individuals (Group IV) fed chiefly on fish flesh, fins and scales, and small whole fish. Small fish taken whole included characids (*H. marginatus* and *O. pulcher*), a curimatid (*C. metae*), and a small loricariid catfish. Pieces of fish flesh identified were from a characid (*A. erythrurus*), a curimatid, a cichlid (*M. ramirezi*), a gymnotoid eel, and an unarmored catfish. The only fin identified was from an armored catfish. Shrimp and crabs were also eaten.

Serrasalmus rhombeus (Linnaeus 1766).—Juvenile *S. rhombeus* have a somewhat elongate body and sharp snout (Fig. 1). They resemble *S. irritans* in body form, but are slightly more robust. Adults have heavy rhomboidal bodies. The body and fins of large individuals, some well over 300 mm SL, are black or blue-black, and the iris is often deep red. They are uncommon in flooded savanna, although on several occasions adults were taken in large numbers by hook and line at night in Caño Maporal.

Juvenile *S. rhombeus* in Groups II–IV specialized on fish fins (Table 5 and Fig. 3). Aquatic insects, mostly plecopterans, were packed in the guts of several specimens from Caño Guaritico. The ten largest *S. rhombeus* (Group V) had taken almost equal volumes of whole small fish, chunks of fish flesh, and fish fins. Fishes identified from the stomachs of larger *S. rhombeus* included characins (*Astyanax bimaculatus* and *Charax* sp.) and the fins of a large fish, possibly *Hoplias*. Three large *S. rhombeus* collected at night in Caño Maporal contained whole or partial individuals of small (20–30 mm SL) doradid catfishes. One individual had eaten a small adult frog.

Serrasalmus cf. elongatus Kner 1860.—*S. cf. elongatus* is a pikelike piranha (Fig. 1) and uncommon in our samples. We examined 42 individuals, including a few from the small size class (Group II) from other locations

TABLE 5. *Food items of* Serrasalmus rhombeus *by size class. %O = percent frequency of occurrence (nonempty stomachs), %D = percent dominance, %V = percent adjusted volume. N = 51.*

Size class (mm SL)	II (20–39)			III (40–79)			IV (80–159)			V (≥160)		
No. examined	18			15			8			10		
No. empty	1			0			1			1		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	—	—	—	20.0	—	—	42.9	25.0	27.3	11.1	—	—
Microcrustacea	23.5	15.8	10.9	—	—	—	—	—	—	—	—	—
Aquatic insects	47.1	26.3	32.6	—	—	—	14.3	—	—	11.1	—	—
Other inverts	5.9	—	—	—	—	—	28.6	12.5	9.1	33.3	—	—
Sm whole fish	—	—	—	6.7	5.9	8.6	—	—	—	44.4	33.3	36.9
Fish flesh	—	—	—	13.3	11.8	8.6	28.6	12.5	18.2	55.6	22.2	21.1
Fish fins	64.7	57.9	56.5	93.3	76.5	80.0	71.4	50.0	45.5	33.3	33.3	31.6
Fish scales	—	—	—	26.7	5.9	2.9	42.9	—	—	22.2	—	—
Other	—	—	—	—	—	—	14.3	—	—	11.1	11.1	10.5

TABLE 6. *Food items of* Serrasalmus cf. elongatus *by size class.* %O = *percent frequency of occurrence (nonempty stomachs),* %D = *percent dominance,* %V = *percent adjusted volume.* N = 42.

Size class (mm SL)	II (20–39)			III (40–79)			IV (80–159)			V (≥160)		
No. examined	3			13			21			5		
No. empty	0			0			1			0		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	—	—	—	23.1	—	—	30.0	5.0	4.5	40.0	—	—
Decapoda	—	—	—	—	—	—	5.0	5.0	2.3	—	—	—
Other inverts	33.3	—	—	—	—	—	15.0	5.0	4.5	—	—	—
Sm whole fish	—	—	—	—	—	—	10.0	10.0	9.1	20.0	—	—
Fish flesh	—	—	—	15.4	12.5	15.6	35.0	30.0	40.9	80.0	40.0	25.0
Fish fins	100.0	100.0	100.0	76.9	50.0	57.8	40.0	20.0	18.2	40.0	20.0	37.5
Fish scales	—	—	—	84.6	37.5	26.6	50.0	20.0	18.2	80.0	40.0	37.5
Other	—	—	—	—	—	—	5.0	5.0	2.3	—	—	—

in the llanos (Table 6 and Fig. 3). Stomachs of three small juveniles (20–39 mm SL) were packed with fins of other small fishes, and one contained a nematode (possibly a parasite). Stomachs of large specimens contained fish fins and many scales. In addition, small whole fish and chunks of fish flesh were taken by the largest *S.* cf. *elongatus.*

Serrasalmus altuvei Ramírez 1965.—*S. altuvei* is a rare, small- to medium-sized piranha with deep narrow body and a slender pointed snout (Fig. 1). It has a silver body and a broad, black terminal band on its unpaired fins. None of our specimens had any red. We examined the stomach contents of 10 of the 17 collected in Caño Maporal and the flooded savanna. Fish fins, scales, flesh, and small whole fish were found in the two size classes (III and IV) represented in our samples. Food items by size class were as follows (%O–%D–%V): Group III (*N* = 3)—small whole fish 33.3–33.3–50.0, fish flesh 33.3–0–0, fins 66.7–66.7–50.0; Group IV (*N* = 7)—plant material 28.9–0–0, fish flesh 42.9–30.0–50.0, fins 71.4–40.0–31.3, scales 42.9–30.0–18.8, other 14.3–0–0.

Pristobrycon cf. striolatus (Steindachner 1908).—*P.* cf. *striolatus* is an uncommon, small- to medium-sized species. In the study area it was collected only in Caño Maporal. Adults have a red-orange chest, occasionally showing a pattern of orange vertical bars along the sides, a rather blunt snout, but much smaller and weaker jaws and jaw musculature than *P. notatus* (Fig. 1). The body is deep but strongly compressed. Small juveniles are similar to young *S. rhombeus* but are slightly stouter, lack ectopterygoid teeth, and have little if any side spotting. The largest individual collected was 159 mm SL. We examined the stomach contents of 16 of the 38 specimens collected (Fig. 3). Specimens in Group II fed mostly on fish fins, as did the one Group III specimen examined. Three adults from Group IV contained fish flesh, a few scales, shrimp fragments, an adult aquatic beetle, an aquatic hemipteran, and unidentified insect fragments. Food items by size class were as follows (%O–%D–%V): Group II (*N* = 12, 1

empty)—aquatic insects 27.3–18.2–13.3, other invertebrates 9.1–0–0, fish flesh 18.2–9.1–10.0, fins 81.8–72.7–76.7; Group III (*N* = 1)—fish fins 100.0–100.0–100.0; Group IV (*N* = 3)—decapoda 66.7–33.3–28.6, aquatic insects 66.7–0–0, other invertebrates 33.3–33.3–28.6, fish flesh 33.3–33.3–42.9, scales 33.3–0–0.

Catoprion mento (Cuvier 1819).—*C. mento* is a small, deep-bodied fish (Fig. 1), usually less than 80 mm SL adult size, and distantly related to the other piranhas. The teeth of *C. mento* are somewhat everted, and its long lower jaw swings open to more than 180 degrees, making it well suited for scraping scales off other fish. The stomachs of all 104 specimens examined contained fish scales (≤23 mm in diameter) (Table 7 and Fig. 3). Plant material—primarily vascular debris and root wads, occasionally filamentous algae—was present in small amounts in many stomachs. Rare items included an aquatic beetle larva, a cladoceran, and the head of a small characid fish (*A. erythrurus*).

COMPARISON OF FOOD HABITS.—Fish (flesh, fins, scales, and small whole fish) were the main components of diets of all eight species of piranhas, both in dominance and adjusted volume (Fig. 3). Only in small juveniles of Group I and juvenile *P. notatus* less than about 80 mm SL (or where sample sizes were small, e.g., Group IV *P.* cf. *striolatus*) did nonfish items make up a large proportion. The majority of juveniles had eaten mostly fish fins. Major exceptions were *P. notatus,* a generalist, and *C. mento,* a highly specialized scale eater. Fins were usually from fishes similar in size to the predator. Thus, juvenile piranhas were attacking small species or juveniles of other fishes. Plant material was usually not important, but was the bulk of stomach contents in a few individuals.

Diet breadth values were typically higher for the larger size classes (Fig. 3), but *C. mento,* the highly specialized scale eater, had low diet breadth values (1.08 to 1.69) for all size groups. Group III *P. notatus,* with 5.92, had the widest breadth. Diet overlap values for the three most

TABLE 7. *Food items of* Catoprion mento *by size class.* %O = *percent frequency of occurrence (nonempty stomachs),* %D = *percent dominance,* %V = *percent adjusted volume.* N = 104.

Size class (mm SL)	II (20–39)			III (40–79)			IV (80–159)		
No. examined	51			50			3		
No. empty									
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	25.5	2.0	2.1	50.0	19.0	16.1	33.3	33.3	28.6
Microcrustacea	2.0	—	—	—	—	—	—	—	—
Aquatic insects	2.0	—	—	—	—	—	—	—	—
Other inverts	3.9	2.0	1.4	—	—	—	—	—	—
Sm whole fish	—	—	—	4.0	3.4	5.0	—	—	—
Fish flesh	—	—	—	2.0	1.7	2.5	—	—	—
Fish fins	—	—	—	2.0	1.7	0.8	—	—	—
Fish scales	100.0	96.1	96.4	100.0	74.1	75.6	100.0	66.7	71.4

common piranha species by size class (Table 8) show that *P. notatus* had less overlap between size classes than *S. irritans* or *S. caribe.*

FEEDING BEHAVIOR.—In a small clearwater stream, Caño Chaviripa in Bolivar State, one of us (LGN) observed feeding behavior of a young (≤40 mm SL) *S. irritans.* It was shoaling with a group of 20 to 30 characins of similar size. The piranha repeatedly bit pieces out of the fins, usually the tail, of other members of the school. Members of the school showed no sign of alarm at this activity, except for the fish actually bitten. It seems likely that the piranha's similar size and schooling behavior prevented the other characins from recognizing it as a predator. A young *S. caribe* in the same stream relied on ambush, hiding near trunks and often attacking and attempting to seize the fins of large fish (*e.g., Brycon*) passing by. The piranha became obviously excited whenever potential prey approached within range.

In aquaria, fin eaters (*e.g., S. altuvei, S. cf. elongatus,* and *S. irritans*) typically bite off and swallow fins of live fish, but ignore dead or wounded fish lying on the bottom. In streams and pools, piranhas often conceal themselves beneath floating mats of vegetation, where they can observe and attack other fishes. Like most characoids, piranhas are active mainly during the day and near dusk.

TABLE 8. *Diet overlaps among the three most common piranha species by size class based on adjusted volume. Diet overlaps (Schoener 1970) range from 0 (no overlap) to 1 (complete overlap).*

	Size class (mm SL)		
Species	II (20–39)	III (40–79)	IV (80–159)
Pygocentrus notatus vs			
Serrasalmus irritans	0.03	0.30	0.67
P. notatus vs *S. caribe*	0.15	0.58	0.69
S. irritans vs *S. caribe*	0.80	0.89	0.88

However, during several nights (1900–0600 hr), we collected many *S. rhombeus* and *P. notatus* by hook from Caño Maporal. Likewise, in aquaria young *S. cf. elongatus* become very active at night, using the cover of darkness to approach and attack other fishes.

DISCUSSION

The Venezuelan Llanos have a diverse and complex fish fauna (Mago-Leccia 1970). Taphorn and Lilyestrom (1984) reported more than 113 species of 15 families in the study area. Additional collecting has raised the number of species to over 125. The piranha assemblage studied included eight species that differ in adult size, body form, and relative abundance. In general, our results show that food habits and diet diversity of these fishes change with age (Fig. 3), usually shifting from fin eating as juveniles to a more generalized mostly piscivorous diet later in life. The major exceptions are *C. mento,* which is a scale eater in all size classes, and *P. notatus,* which preys on a wide variety of organisms as a juvenile. Juvenile piranhas, Groups I through III, fall into three trophic units: generalists (*Pygocentrus*), scale eaters (*Catoprion*), and fin eaters (*Serrasalmus* and *Pristobrycon*).

Our data on differences in food habits among different size classes of a given species support the contention of Stoner and Livingston (1984) that ecological studies of fishes should employ the "ontogenetic trophic unit" concept rather than grouping a taxonomic species as a single functional ecological unit. Nevertheless, some piranhas show flexibility within a size class. For example, juveniles of *S. rhombeus,* typically fin eaters, were full of aquatic insects in one sample.

Because Roberts (1970) and Goulding (1980) found *S. elongatus* to be primarily a scale and fin eater, we suspected that other pointed-snout species would have similar habits. Furthermore, we expected that blunt-snouted species (*Pristobrycon, Pygocentrus,* and *S. caribe*) would feed more on fish flesh. *Pygocentrus* fit our predictions, but a clear correlation between morphology and diet in

Serrasalmus and Pristobrycon was not found. Juvenile Pristobrycon fed on fins in proportions comparable to Serrasalmus; and adult Serrasalmus, like Pristobrycon and Pygocentrus, were general piscivores, taking primarily small fish and fish flesh as well as fins and scales. However, young of both Serrasalmus and Pristobrycon were proportionally longer bodied relative to body depth, and with snouts usually more elongated and pointed than adults, with different levels of variation depending on species. An extreme example of this is S. rhombeus, whose change in body form with age has been described and figured by Géry (1972). Vieira and Géry (1979) reported that C. mento shifted diets from insects and plant material when young to fish scales when adult. However, we found C. mento of all sizes to be scale specialists.

Goulding (1980) hypothesized that scale and fin eating is the "primitive" or ancestral ecological character state for piranhas, later giving rise to flesh eating (see Northcote et al. 1986b). Data on juvenile diets (Sazima & Zamprogno 1985; Northcote et al. 1986b, pers. obs.) support his view if we can assume that ecological traits of juveniles are more primitive than those of adults. However, the smallest piranhas (Group I), like many other characoids, take mostly invertebrates. Other serrasalmines, e.g., Piaractus and Colossoma (which are herbivores or frugivores as adults), have juveniles that eat microcrustaceans (Machado-Allison 1982). Sazima (1984) suggested that scale eating (lepidophagy) arose from trophic (e.g., modified piscivory) or social (e.g., intra- and interspecific aggression) behaviors. These may also be involved in the origin of fin eating. Feeding tactics of the various species of fin eaters may be species specific. Our field and aquarium observations show various feeding strategies for different piranha species, and in nature they probably differ in types of fish preyed on.

In any case, fin eating is a common and widespread feeding adaptation in Venezuelan freshwater fishes, and indirect evidence (i.e., fish with missing or damaged fins) is found in almost all fish samples from the llanos. Many species may eat fins because fins are an abundant and rapidly renewable resource (Northcote et al. 1986b, pers. obs.). In aquaria, fishes from the llanos regenerate damaged fins in a matter of days. In cropping fins instead of eating the whole animal, piranhas resemble herbivores that continually exploit their food resource without eliminating it (see Northcote et al. 1986b). Reproduction of piranhas is closely correlated with the reproductive cycle of most other llaneran fishes. Thus, there is an abundance of small prey available to young fish predators.

Mago-Leccia (1970) and Machado-Allison (1982) suggested that similarities in body shape and coloration between P. notatus and the young of the vegetarian serrasalmine Piaractus may represent mimicry. Juveniles of fin-eating S. irritans appear to practice aggressive mimicry, much like that which Sazima (1977) suggested for the scale-eating characin Probolodus heterostomus. Our field observations show that young S. caribe often rely on ambush and short chases to feed on fins. Piranhas also may linger near prey, as if not interested, and then attack from close range (Sazima 1984) (e.g., S. cf. elongatus, pers. obs.).

If numbers of individuals, biomass, and distribution are criteria for measuring the adaptive success of a species, then P. notatus is by far the most successful piranha in the llanos. It also has the most generalized diet. Only in nutrient-poor black waters, where clarity is high and biomass often low, is P. notatus rare or absent. Its success may be a result of its highly opportunistic feeding strategy, an advantage in a seasonal and usually unpredictable environment.

Goulding (1980) found that large adult Amazonian S. elongatus had highly specialized diets of mainly scales and fins. Our few specimens of S. cf. elongatus, all over 160 mm SL, were more generalized, taking flesh and small fish as well as fins and scales. The dominant Amazonian piranha, S. rhombeus, preyed most heavily on common fishes of about its own size by removing chunks of flesh (Goulding 1980). No small fish were identified as prey items. We found whole small fish to be a major food item for many of the large piranhas. Differences between our findings and those of Goulding may be related to differences in biomass between rich llanos water bodies and nutrient-poor rain forest streams. Goulding studied primarily large fishes collected by gill nets; thus, his piranhas probably were attacking other large fishes entangled in gill nets until they themselves were caught. Stomach contents from such fish would be skewed toward fish flesh. With the use of seines, especially of small mesh size, piranhas have the opportunity to attack small fishes driven out of microhabitats that would normally afford some safety. Thus, our study was partly biased toward small fishes being eaten, but large fish were also driven in front of seining nets. Therefore, feeding piranhas still had opportunities to select either large or small prey.

Stomachs of several species of piranhas from Amazonian rain forests contained large amounts of masticated seeds and some fruits (Goulding 1980). Cyperacean seeds were found to be one of the principal food components of juvenile piranhas from the flooded central llanos of Guárico State (Machado-Allison & Garcia 1986), but information on volume and numbers of seeds eaten was not provided. We rarely found evidence of seed eating by piranhas in the llanos, and any seeds eaten were very small and may have been taken secondarily along with intended prey items. Although other plant material, such as bits of leaves, grass blades, root wads, tiny flowers, and filamentous algae, were ingested, these items were usually of minor importance in both dominance and volume. Of hundreds of specimens examined, not one stomach contained many seeds. Most of the western llanos, including gallery forests, do not produce much large fruits or big seeds. By way of comparison, stomachs of the herbivorous adults of My-

lossoma sp. and *Metynnis* sp. taken in the study area were typically full of filamentous algae, masticated small seeds, or nonwoody vascular plant debris.

Géry (1963) suggested a parallel evolution, in which sharp-snouted piranhas somehow benefited from association with the more aggressive blunt-headed and robust species such as *Pygocentrus*. He based this hypothesis on the simple observation of their frequent co-occurrence. We have noted that large shoals of medium-sized juvenile *P. notatus* always contain a few juveniles of one or more of the sharp-snouted species, usually *S. irritans*. Whether these fin eaters are participating in the attack, recovering bits of flesh or fins that result, or are attacking the other tightly packed piranhas is not known. We often collected three species of piranhas (*P. notatus, S. irritans,* and *S. caribe*) from beneath the same mat of floating aquatic vegetation. On rare occasions we took as many as five species in one short seine haul. Water hyacinth mats provide both shelter and foraging areas for young piranhas (Sazima & Zamprogno 1985, pers. obs.).

A clear understanding of competitive interactions among piranhas is complicated by syntopy of many other medium- and large-sized predatory fishes. In the study area these included ageneiosid and pimelodid catfishes of the genera *Ageneiosus, Pimelodus, Phractocephalus, Pseudoplatystoma,* and *Pseudopimelodus*; large characoids (*Hydrolycus, Hoplias,* and *Boulengerella*); the peacock cichlid (*Cichla ocellaris*); a freshwater drum (*Plagioscion*); and the electric eel (*Electrophorus electricus*). Caimans (*C. crocodilus*) and fish-eating birds are also very common.

Several researchers (*e.g.,* Lowe-McConnell 1964, 1975; Mago-Leccia 1970; Welcomme 1979) found that many freshwater fishes of the tropics reduce or stop feeding during the dry season. Although food for small predators may be limited during low water (*e.g.,* Nico & Taphorn 1985), our study does not provide evidence of major seasonal diet shifts nor a significant reduction in feeding by piranhas. Goulding (1980) also found food of larger carnivorous fishes to be less affected by seasonality. Nevertheless, extremely harsh or dry years may provide contrary evidence. Large predators in our study area did not seem to be food limited, even in the dry season. Most fishes reproduce early in the rainy season, so most sites contain an abundance of small fishes throughout the wet period. Fish density is even higher during the dry season because of greatly reduced water volume. Considerable diet overlap among some piranha species in the same size classes suggests that interspecific competition for plentiful food resources is not very important.

ACKNOWLEDGMENTS

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